J Neurophysiol 98: 1405–1414, 2007.
First published June 6, 2007; doi:10.1152/jn.00132.2007.

Target Acceleration Can Be Extracted and Represented Within the Predictive Drive to Ocular Pursuit

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[1]*Research Institute for Exercise and Sport Sciences, Liverpool John Moores University, Liverpool;* [2]*Faculty of Life Sciences, University of Manchester, Manchester, United Kingdom; and* [3]*Center for Systems Engineering and Applied Mechanics and* [4]*Laboratory of Neurophysiology, Université Catholique de Louvain, Brussels, Belgium*

Submitted 6 February 2007; accepted in final form 4 June 2007

Bennett SJ, Orban de Xivry J-J, Barnes GR, Lefèvre P. Target acceleration can be extracted and represented within the predictive drive to ocular pursuit. *J Neurophysiol* 98: 1405–1414, 2007. First published June 6, 2007; doi:10.1152/jn.00132.2007. Given sufficient exposure to stimulus presentation, the oculomotor system generates a representation of the stimulus characteristics, which is then used to predict the upcoming target motion. In addition to compensating for the perceptual-motor delay, these predictive processes perpetuate eye motion during a transient occlusion and compensate for the loss of visual input. At present, however, it is not well understood whether and how the oculomotor system extracts and represents target acceleration for subsequent predictive control. To this end, we used a target occlusion paradigm where both position and velocity of the target during the occlusion and at reappearance could not be predicted without extracting target acceleration before target disappearance. We found that the oculomotor response during the blanking period was not influenced by target acceleration when the initial exposure was 200 ms. However, smooth and saccadic eye movements did discriminate between the different levels of acceleration after an initial 500- or 800-ms exposure. In the event that the smooth response during the occlusion did not match well the target trajectory and thus eliminate a developing displacement error, there was an increased saccadic displacement. Still, the combined response during the blanking period did not eliminate retinal slip and position error at target reappearance. These results indicate that information on target acceleration can be extracted on-line, during pursuit of a visible ramp, and then used to drive a predictive oculomotor response in the absence of visual input.

INTRODUCTION

As we move around and interact within our natural surrounds it is common to experience accelerating object motion. It is therefore not difficult to think of situations where there is potential for serious consequences if the effect of object acceleration is not perceived and acted on. For example, misperceiving the changing relationship between two approaching cars can lead to an incorrect braking strategy, possibly resulting in a collision (Lee 1976). Less-severe consequences are evident in interceptive tasks such as pointing and reaching (Brouwer et al. 2003; Port et al. 1997), but still successful performance is dependent on maintaining a precise relationship between the observer and moving object. Physiological and psychological research indicates that these human behaviors are supported by a visual system that constitutes highly specific motion-processing mechanisms capable of extracting information about an object's direction and speed (Anderson and Burr 1985; McKee 1981; Watamaniuk and Heinen 1999). Interestingly, however, the human visual system is less capable of discriminating object acceleration (Snowden and Braddick 1991; Watamaniuk and Heinen 2003; Werkhoven et al. 1992). This is consistent with the finding that in response to target acceleration the firing of neurons in MT, the key motion processing area of the monkey, is not independent of target speed (Lisberger and Movshon 1999; Price et al. 2005). In fact, the general consensus is that humans do not perceive acceleration directly, but rather perceive acceleration indirectly from change in speed. This conclusion is further supported by psychophysical studies, which have shown that perceptual discrimination of acceleration is influenced by mean velocity over a presentation (Brouwer et al. 2002; Gottsdanker et al. 1961; Schmerler 1976) and thus is not simply dependent on the magnitude of acceleration per se. For instance, for two presentations of equal duration (e.g., 500 ms) with the same target acceleration (e.g., 8 deg/s^2) but different initial and final velocities (e.g., 8 and 12 deg/s; 24 and 28 deg/s), the former would be more readily discriminated as containing accelerative motion because the percentage change in velocity [i.e., (initial velocity − final velocity)/mean velocity; 41 and 16%, respectively] is well above the reported threshold of 25%.

Although sensitivity to the effect of acceleration on object motion conveys significant advantage, the need to sample and compare object speeds (for a physiological model based on population coding of MT neurons see Lisberger and Movshon 1999) could be responsible for the high acceleration discrimination threshold. In other words, whereas speed discrimination has a low threshold enabling detection of speed differences of $<5\%$ (McKee 1981), the process of extracting reliable information on object acceleration appears to introduce error (for a discussion of possible mechanisms see Watamaniuk and Heinen 2003). This process has been shown to be influenced by presentation duration, with estimates of about 100 ms being required to differentiate the speed signal (Werkhoven et al. 1992) and 300 ms being sufficient for perception to correctly discriminate a 25% between-trial change in velocity arising from constant acceleration on 75% of trials (Brouwer et al. 2002). It is thus likely that the inadequacy of acceleration extraction over short stimulus duration accounts for the lack of scaling in the open-loop period of smooth pursuit (i.e., 40–140

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ms after onset) to the target velocity resulting from acceleration (Watamaniuk and Heinen 2003).

As a result of poor discrimination of target acceleration over short stimulus presentations, it follows that there will be significant retinal slip and position error both during and after the open-loop period of smooth pursuit. To avoid the mismatch between eye and target motion, it has been suggested that, given sufficient exposure, the oculomotor system uses a corollary discharge mechanism (Robinson et al. 1986) that provides a reference (e.g., efference copy) to predict the ongoing eye movement. To date, however, although these models of ocular pursuit have incorporated input of an acceleration signal that influences the latency of pursuit onset (Krauzlis and Lisberger 1994), the efference copy has typically been modeled to represent an eye-velocity signal of constant magnitude. Recognizing the limitations of such models, others have suggested that a more persistent velocity-based memory can be formed, given sufficient opportunity to sample and hold the stimulus characteristics, and that this can account for pursuit of sinusoidal target motion (Barnes and Asselman 1991). Recent refinement of this latter model has led to the proposal that the velocity-based representation is in fact tuned with a variable gain function to produce drive with the desired acceleration characteristics (Bennett and Barnes 2006).

Despite attempts to examine pursuit of accelerating target motion there remains a clear need to more fully determine the sensitivity of the oculomotor system to target acceleration. Work on the latency to initiate pursuit (Krauzlis and Lisberger 1994) and the subsequent 40- to 140-ms open-loop response (Watamaniuk and Heinen 2003) cannot verify whether the extraction of an acceleration signal that inputs to ocular pursuit improves over a stimulus duration longer than the perceptual-motor delay, and whether this then forms the basis of a predictive response. Further, because only targets with positive acceleration were used, it remains unknown whether, like perceptual discrimination (Babler and Dannemiler 1993; Calderone and Kaiser 1989; Gottsdanker et al. 1961; Schmerler 1976), ocular pursuit also discriminates between negative acceleration and positive acceleration. Longer ramps of accelerating target motion were given in the study of Bennett and Barnes (2006). However, because stimulus presentation was arranged to enhance predictability, it was not possible to confirm whether the increase in smooth pursuit during the transient target occlusion reflected a prediction made in advance of target motion regarding the expected change in target velocity either side of the occlusion or an on-line extraction and representation of the acceleration signal made during pursuit of the initial visible ramp. Finally, to date none of the studies on pursuit of accelerating target motion has examined the collaboration between the two oculomotor subsystems: saccades and smooth pursuit (for reviews see Krauzlis 2004; Krauzlis and Stone 1999). This is an important omission because the combined response of saccades and smooth pursuit during transient occlusion can reveal much about how precisely the oculomotor system represents a target's trajectory (Orban de Xivry et al. 2006).

Herein we report the results of a study in which we examined smooth and saccadic pursuit during a transient target occlusion where target acceleration and deceleration, initial target velocity, and visible duration before target occlusion were randomized across trials. By maintaining a fixed start position, this combination of parameters enabled us to decorrelate target position and velocity just before occlusion, as well as mean target velocity during the initial visible ramp, from target acceleration. Thus the design enabled us to determine whether the pursuit response during a transient occlusion was based on a measure of target acceleration or target velocity. According to the standard efference copy model of pursuit, eye motion during an occlusion is based on target velocity just before occlusion. In our protocol, the preocclusion target velocity was independent of target acceleration. Therefore there should be no relationship between the oculomotor response and target acceleration if extrapolation were based on preocclusion target velocity. Consequently, we will refer to this as the "final velocity" hypothesis. Instead of extrapolating eye motion using the preocclusion target velocity, subjects could use a more global measure of target velocity—that is, mean target velocity during any earlier interval of the initial visible ramp. To reveal any evidence for this effect, we designed the target parameters in such a way that average target velocity was negatively correlated with target acceleration ("average velocity" hypothesis). Finally, if the oculomotor response during the occlusion were based on target acceleration during the initial visible ramp, it would be positively related to target acceleration ("acceleration" hypothesis).

METHODS

Experimental setup

Six healthy human subjects (mean age: 27 yr), all of whom had previous experience of ocular pursuit tasks, participated after giving informed consent. Two of the subjects were authors (S3, S5) and the others were naïve to the purpose of the study. All subjects had normal or corrected-to-normal vision, were healthy, and without any known oculomotor abnormalities. All procedures were conducted with approval of the Université Catholique de Louvain ethics committee.

Subjects sat in a purpose-built dark room, facing a flat white screen (2×1.5 m) at a viewing distance of 1.5 m. The head was supported with a chin rest that was adjusted to each subject's height. Visual stimuli were projected onto the screen using a CRT projector (Barco Cine8) with a refresh rate of 100 Hz and 800×600 spatial resolution. The horizontal motion of the visual stimuli was controlled by a visual stimulus generator (VSG2-5; Cambridge Research Systems) interfaced with a PC running proprietary software through MATLAB (The MathWorks). Eye movements were recorded at 200 Hz using a Chronos eye tracker (Skalar Medical BV) and stored to a PC for off-line analysis.

Paradigm

We performed a standard occlusion experiment over four sessions, each lasting about 30 min. Each session began with a calibration procedure (see Orban de Xivry et al. 2006) followed by blocks of 40 presentations that were received in a pseudorandom order. A presentation began with a green central fixation point presented for a period varying randomly between 500 and 1,500 ms. After the fixation period, the green target was replaced by a co-located red target that started to move at constant acceleration either leftward or rightward for 200, 500, or 800 ms, after which the target disappeared behind an imaginary occluder for 800 ms. Initial target velocity was chosen such that target velocity 50 ms before occlusion (preocclusion velocity) was either 0 or 8 deg/s (in absolute value). Target acceleration was constant during the entire presentation; thus when the target reappeared for 400 ms after the occlusion its motion characteristics were a straightforward extrapolation of the previous trajectory. For preoc-

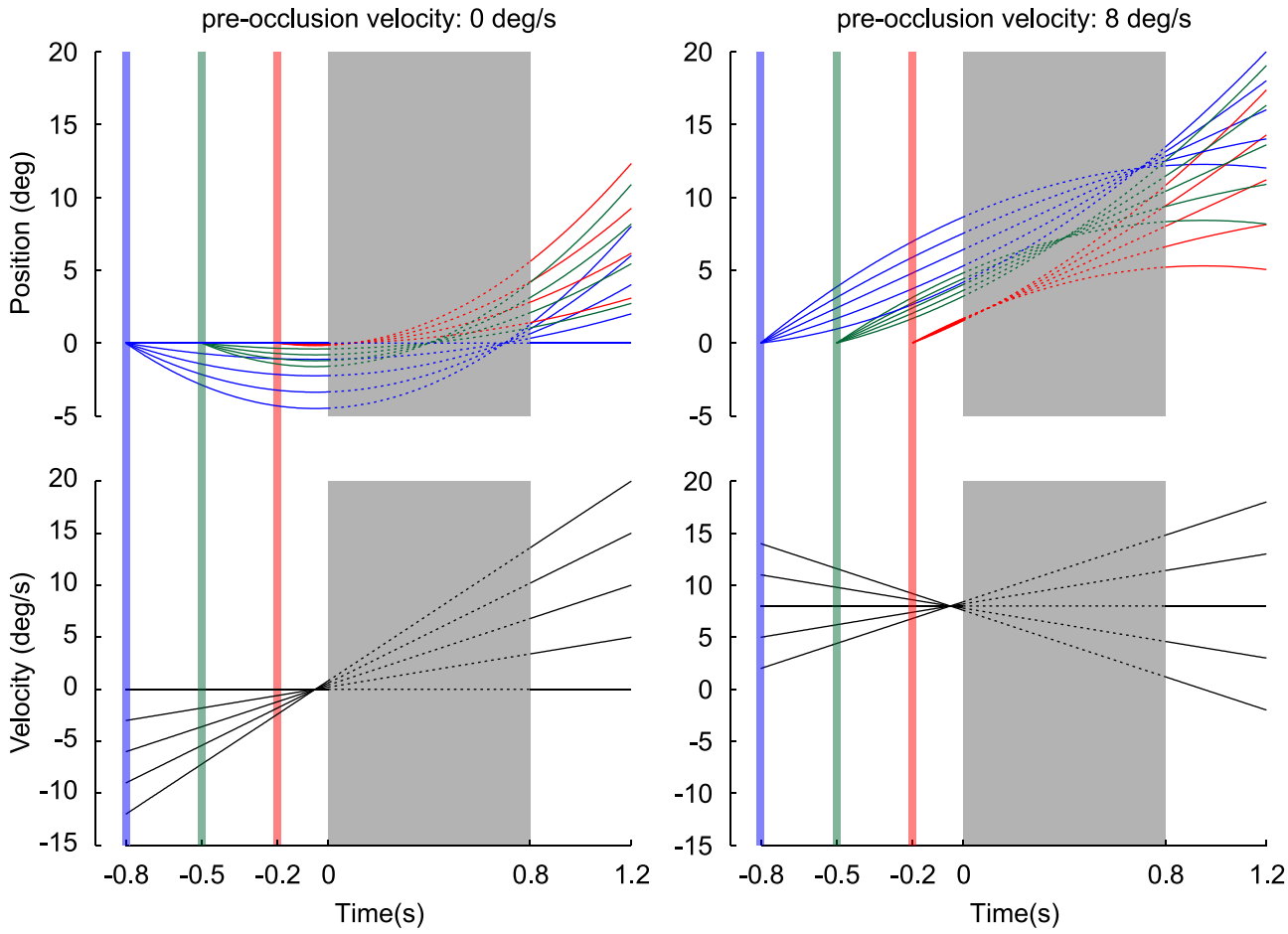

FIG. 1. Representation of pursuit target position (vertical axis in *top panels*) and velocity (vertical axis in *bottom panels*) vs. time (horizontal axis). Target motion onset is indicated by the thick vertical line. At this time the red pursuit target became visible and moved for 200 ms (red), 500 (green) or 800 ms (blue) with velocity and acceleration characteristics that brought it to preocclusion velocity of 0 deg/s (*left-side panels*) or 8 deg/s (*right-side panels*). Target was then occluded for 800 ms (light gray shaded area) and finally reappeared for a further 400 ms. Target acceleration was 0, 4, 8, 12, or 16 deg/s^2 for 0 deg/s preocclusion velocity (*left*) and −8, −4, 0, 4, or 8 deg/s^2 for 8 deg/s preocclusion velocity (*right*). Combination of preocclusion target velocity and target acceleration resulted in 10 distinct position trajectories for each initial ramp duration.

clusion target velocity of 8 deg/s, target acceleration was −8, −4, 0, 4, or 8 deg/s^2, whereas for the preocclusion target velocity of 0 deg/s, target acceleration was 0, 4, 8, 12, or 16 deg/s^2 (see Fig. 1). Subjects were instructed to track the horizontal target as accurately as possible throughout the presentation.

Our protocol was designed to disambiguate the different parameters that subjects could use to extrapolate target motion during the occlusion. Therefore the two different levels of preocclusion target velocity were independent of target acceleration. Moreover, the mean target velocity during any interval of the initial visible ramp (apart from the final 50 ms) was negatively related to target acceleration; so was target position at target disappearance. In total, there were 60 different conditions (2 preocclusion velocities × 2 directions × 3 ramp durations × 5 levels of acceleration) that were presented, on average, 15 times over the four sessions. This minimized the predictive influence of cues (e.g., start velocity of the initial visible ramp, target position at the end of the first ramp) that were ambiguously related to target acceleration. Consequently, our protocol enabled us to discriminate between three potential hypotheses for extrapolating the oculomotor response during a transient occlusion.

Data analysis

Eye and target position signals were low-pass filtered at 50 Hz using an autoregressive, zero-phase digital filter implemented in MATLAB. Eye velocity and acceleration were derived from filtered position signals using a weighted central-difference algorithm on a ±10-ms time interval. Saccades were detected using a 500 deg/s^2 acceleration threshold and were considered to occur during the occlusion when their onset was ≥100 ms after the start of the occlusion and before its end. The smooth component of the saccadic amplitude was removed using a technique described in de Brouwer et al. (2002). The computation of the smooth component was obtained by multiplying the saccade duration by the mean smooth eye velocity during the saccade. The raw saccade amplitude data were then corrected by subtracting the smooth component. The total contribution of the saccadic system to the displacement (SAD) during the occlusion interval was obtained by summing the signed amplitude of all the saccades. To obtain desaccaded smooth eye velocity, we then removed the identified saccades plus five additional data points (equivalent to 25 ms) at the beginning and end of the identified saccade trajectory from the eye velocity trace. The removed data were replaced by a linear interpolation routine based on the smooth eye velocity before and after the saccade (for more details see de Brouwer et al. 2002). The contribution of the smooth pursuit system to the displacement (SED) during the occlusion interval was obtained by integrating the smooth eye velocity during this interval. The total eye displacement during the occlusion was computed from the sum of SAD and SED.

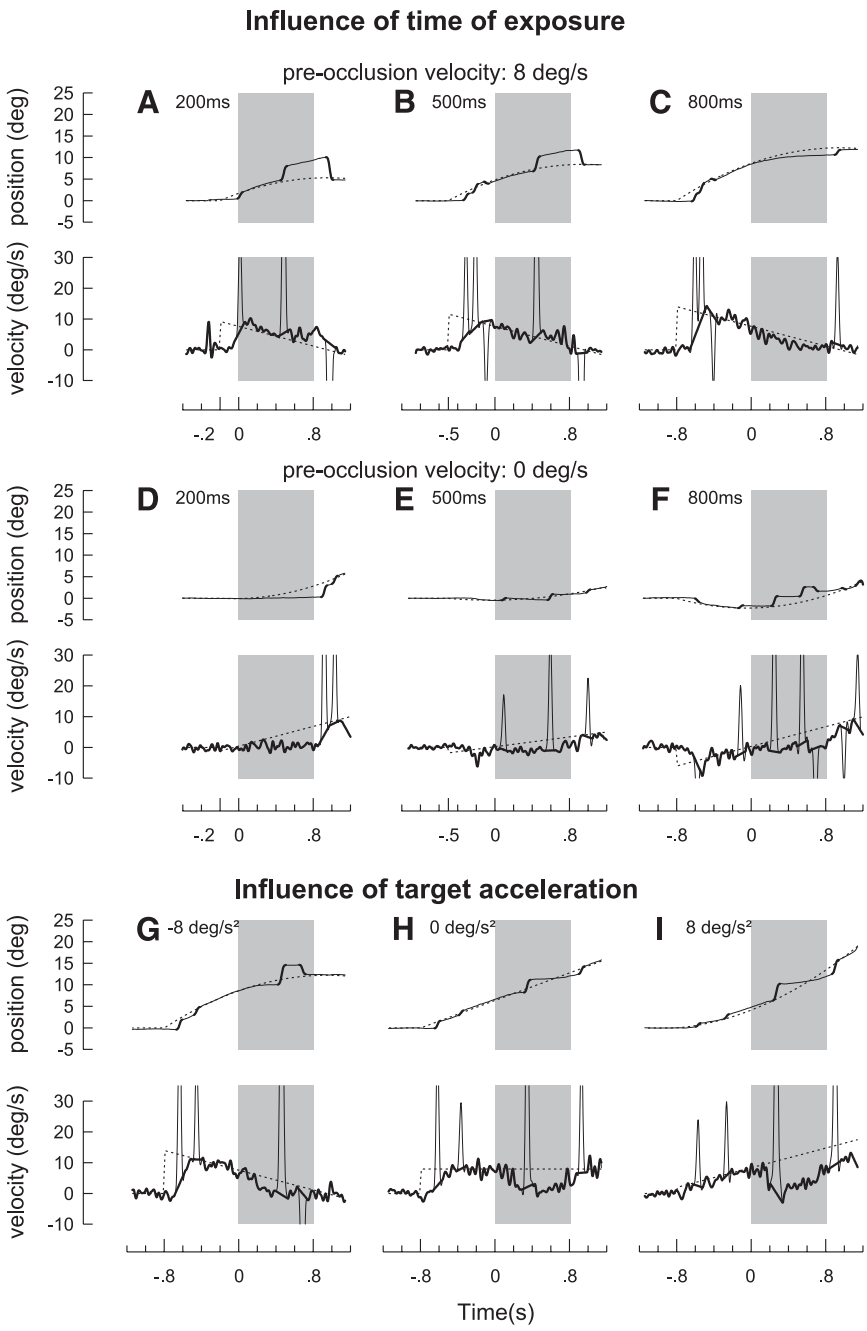

FIG. 2. Representative examples from a single subject (S5) of the position (deg) and velocity (deg/s) vs. time (s) of the eye (continuous traces) and target (thin broken traces). In the eye position traces, the thick parts represent identified saccades. On the eye velocity panels, thick traces represent desaccaded smooth eye velocity and thin traces indicate saccades. In the *top* and *middle set* of plots for preocclusion velocity 8 deg/s (*A*, *B*, *C*) and 0 deg/s (*D*, *E*, *F*), target acceleration is 8 deg/s^2. In the *bottom set* of plots (*G*, *H*, *I*) preocclusion velocity is 8 deg/s and initial ramp duration is 800 ms. Target occlusion is represented by the light gray shaded area.

For the purposes of statistical analysis, we calculated intrasubject means for selected measures of the smooth and saccadic eye movements during a presentation. Data from presentations with 0 deg/s preocclusion velocity and 0 deg/s^2 acceleration were not included in the analysis. These presentations were included in the design to reduce anticipatory eye movements before target motion onset and to discourage subjects from simply responding with an eye movement of equal magnitude irrespective of target acceleration. Additionally, data were average from presentations with leftward and rightward target motion during the occlusion. Because there were different numbers of target accelerations where preocclusion target velocity was 0 or 8 deg/s, the intrasubject mean data for these presentations were submitted to separate ANOVAs. Main and interaction effects were quantified using Tukey's HSD post hoc procedure; this test performs all comparisons while maintaining alpha and the probability of making a type I error at the specified level. Finally, regression analyses were used to more fully explore the relationship between target acceleration and our dependent measures. To this end, the intrasubject mean data were regressed against corresponding target data; this was done separately for each initial ramp duration.

RESULTS

Typical examples

Representative examples of the pursuit response on individual trials to various stimulus characteristics are shown in Fig. 2. As expected—given the variability in fixation period combined with unpredictability of the upcoming target speed, acceleration, and direction—subjects exhibited very little (if any) anticipatory eye movements (smooth or saccadic). Following pursuit onset, the eyes tracked the target with a com-

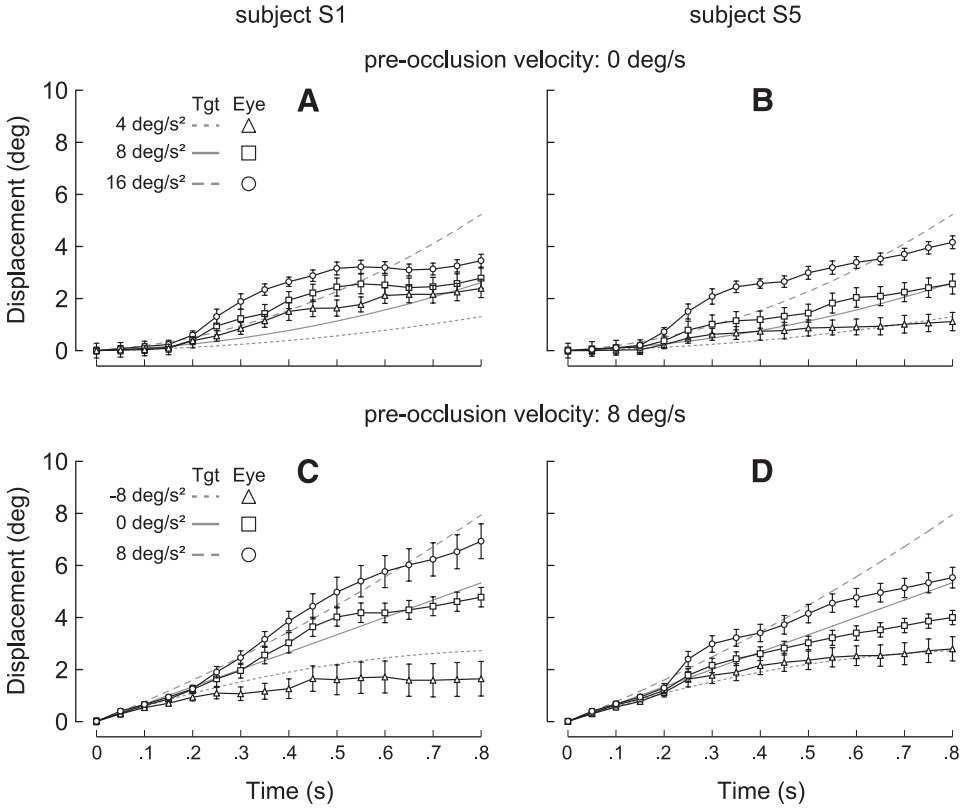

FIG. 3. Representative examples from 2 subjects (*A* and *C*: S1; *B* and *D*: S5) of mean (±SE) eye displacement vs. time (s) for targets with 0 deg/s preocclusion velocity (*top*) and 8 deg/s preocclusion velocity (*bottom*). Initial ramp duration was 800 ms. Pursuit target (*gray traces*) and eye (*black traces* with symbols) displacement are normalized to 50 ms into the start of the occlusion interval to remove influence of visually driven response. Symbols and line style indicate response of eye and target, respectively.

bination of smooth and saccadic movements. Around the moment of target occlusion, eye velocity and position were reasonably well matched to target velocity and position for the 500- and 800-ms ramps (e.g., Fig. 2, *B*, *C*, *E*, and *F*). For these two conditions, preocclusion smooth eye velocity was similar across the range of ramp duration and target acceleration. For the 200-ms ramp (Fig. 2*A*), there was insufficient time for eye velocity to reach a preocclusion velocity of 8 deg/s, whereas there was very little target motion to drive eye motion when the preocclusion target velocity was 0 deg/s (Fig. 2*D*); target displacement was <0.2 deg for each level of target acceleration.

In all presentations where the preocclusion target velocity was 8 deg/s, subjects exhibited substantial eye motion during the initial ramp, which was then continued during the occlusion interval. In general, smooth eye velocity decayed after target disappearance and then recovered before target reappearance. The recovery differed in line with target acceleration (and velocity) when the target had initially been tracked for 500 and 800 ms (e.g., Fig. 2, *G–I*). In presentations where target velocity remained equal or increased during the occlusion interval, eye velocity was not sufficient to eliminate the developing position error and thus was accompanied by forward saccades (e.g., Fig. 2, *E*, *F*, *H*, and *I*). In some instances, the combination of smooth pursuit and forward saccades brought the eye to a position ahead of the target, which was then corrected by reverse saccades; this was particularly evident in presentations with negative target acceleration (Fig. 2, *F* and *G*).

Representative examples from two subjects of total eye displacement resulting from the combined smooth and saccadic response during an 800-ms occlusion interval are shown in Fig. 3. The pursuit response of both subjects discriminated between the different levels of target acceleration, although there was some intersubject variation. For presentations where preocclusion target velocity was 0 deg/s (Fig. 3, *A* and *B*), subject 1 exhibited less variation between the different levels of target acceleration than did subject 5. This was reflected in a total eye displacement for subject 1 that overshot the displacement of a 4 deg/s^2 target and undershot the displacement of a 16 deg/s^2 target. For subject 5, total eye displacement was well matched to target displacement for each level of acceleration. A somewhat reverse pattern was observed in presentations where the preocclusion target velocity was 8 deg/s (Fig. 3, *C* and *D*). Total eye displacement for subject 1 was reasonably well matched to the target displacement corresponding to each level of acceleration, whereas for subject 5 there was considerable undershoot except when pursuing a −8 deg/s^2 target.

End-occlusion smooth pursuit

Having observed in our data the general trend of a reduction in smooth eye velocity during target occlusion followed by a recovery, it was important to segregate this global effect from the influence of target acceleration on the smooth response. We achieved this goal by comparing for each initial ramp duration the average eye velocity at end-occlusion pooled across all acceleration levels (dashed line in Fig. 4) with the response to each acceleration level. This provided a direct way of testing the three proposed hypotheses: *1*) final velocity hypothesis (no modulation), *2*) average velocity hypothesis (negative relationship with target acceleration), and *3*) acceleration hypothesis (positive relationship with target acceleration).

Figure 4 shows the group mean end-occlusion eye velocity for targets with a preocclusion velocity of 0 and 8 deg/s. Here

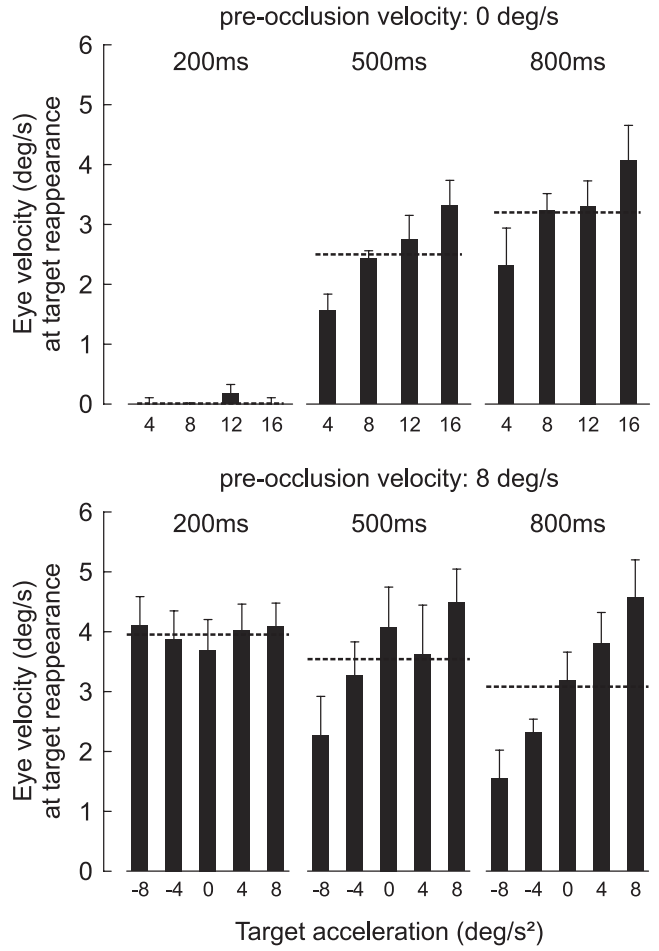

FIG. 4. Group mean (+SE) eye velocity (dark gray bars) at end-occlusion for targets with 0 deg/s preocclusion velocity (*top*) and 8 deg/s preocclusion velocity (*bottom*). Horizontal dashed lines represent the average eye velocity obtained by collapsing the data across all target accelerations. *Left*, *middle*, and *right columns* (i.e., subset of bars) correspond, respectively, to initial ramp duration of 200, 500, and 800 ms. Horizontal axis legends represent target acceleration.

it can be seen that end-occlusion eye velocity remained uninfluenced by target acceleration in presentations where the target was initially visible for 200 ms (Fig. 4, *left column*). This was not the case after pursuing the target for a 500- or 800-ms ramp (Fig. 4, *middle* and *right columns*) where, for both levels of preocclusion target velocity, end-occlusion eye velocity across all target accelerations was modulated positively around average eye velocity. For the 0 deg/s preocclusion target velocity, the modulation of smooth eye velocity with target acceleration was confirmed by ANOVA [significant interaction between ramp duration and target acceleration; $F(6,30) = 2.85$, $P < 0.05$]. In presentations with either 500- or 800-ms ramp duration, end-occlusion eye velocity was significantly higher when pursuing targets with acceleration of 16 versus 4 deg/s^2. For the 8 deg/s preocclusion target velocity, the smooth eye velocity decreased after the start of the occlusion and then recovered, albeit to a level that was below start-occlusion smooth eye velocity. For the two longest initial ramp durations, smooth eye velocity differed as a function of target acceleration [$F(8,40) = 4.61$, $P < 0.01$]. End-occlusion eye velocity was significantly higher when pursuing targets with acceleration of 8 versus -8 deg/s^2.

The scaling of smooth eye velocity according to target acceleration was confirmed by regression analysis. As shown in Table 1, end-occlusion eye velocity did not change in proportion with target acceleration in presentations where the target was initially visible for 200 ms (0 and 8 deg/s preocclusion velocity). After pursuing the target for either a 500- or 800-ms ramp there was a more obvious scaling of end-occlusion eye velocity to target acceleration (0 and 8 deg/s preocclusion velocity). However, the slope of the regression equations indicates the scaling of end-occlusion eye velocity fell well short of unity.

Saccades during occlusion

The total saccadic eye displacement (SAD) during the occlusion was quantified using the same approach as in the previous section [i.e., comparing for each initial ramp duration the average SAD pooled across all target acceleration levels (horizontal dashed lines in Fig. 5) with the response to each acceleration level]. Group mean in Fig. 5 shows that for targets with 0 deg/s preocclusion velocity, there was no modulation of saccadic eye displacement with target acceleration after an initial 200-ms ramp (Fig. 5, *left column*, *top*); there was almost no saccadic response during the occlusion interval. However, there was clear modulation of saccadic eye displacement around the mean after an initial 500- or 800-ms ramp (Fig. 5, *middle* and *right columns*, *top*). This was confirmed by the presence of a significant interaction between ramp duration and target acceleration [$F(6,30) = 2.78$, $P < 0.05$]. Post hoc testing indicated that the saccadic eye displacement during the transient occlusion was significantly greater when pursuing targets with acceleration of 16 versus 4 deg/s^2. These effects were also evident in the regression analysis, which showed that saccadic eye displacement changed in proportion with target acceleration in presentations where the target was initially visible for 500 or 800 ms (Table 1).

For targets with 8 deg/s preocclusion velocity there was a less-obvious modulation of saccadic eye displacement to target acceleration (Fig. 5, *bottom*), although, contrary to the response to targets with 0 deg/s preocclusion velocity, there was a notable contribution from saccades during the occlusion after all initial ramp durations. Once again there was a lack of

TABLE 1. *Regression statistics for fit of eye data to target data*

	0 deg/s			8 deg/s		
	R^2	Slope	P	R^2	Slope	P
EV						
200	0.001	0.002	0.90	0.001	0.003	0.94
500	0.310	0.156	0.01	0.146	0.140	0.04
800	0.193	0.148	0.03	0.352	0.212	0.01
SAD						
200	0.014	0.033	0.58	0.001	−0.013	0.83
500	0.577	0.324	0.01	0.048	0.091	0.24
800	0.473	0.385	0.01	0.216	0.211	0.01
TED						
200	0.000	−0.032	0.93	0.006	0.005	0.68
500	0.585	0.230	0.01	0.134	0.411	0.05
800	0.589	0.420	0.01	0.333	0.550	0.01

Degrees of freedom (df) are 22 and 28 for 0 and 8 deg/s preocclusion target velocity, respectively. EV, eye velocity at target reappearance; SAD, saccadic eye displacement; TED, total eye displacement.

modulation of saccadic eye displacement around the mean after an initial 200-ms ramp [significant main effect of initial ramp duration; $F(2,10) = 4.29$, $P < 0.05$]. Figure 5 (*right column*, *bottom*) shows that a difference in saccadic eye displacement during the transient occlusion was evident only between target accelerations of −8 and 8 deg/s^2 in presentations with an 800-ms initial ramp. This less-robust scaling of saccadic eye displacement to target acceleration was confirmed by regression analysis (Table 1). Saccadic eye displacement did not change in proportion with target acceleration in presentations with an initial 200- or 500-ms ramp. Furthermore, although significant, the slope of the regression on presentations with an initial 800-ms ramp was lower than that observed for presentations of the same initial duration and 0 deg/s preocclusion target velocity.

Combination of smooth pursuit and saccades for the control of eye displacement

Having shown that both the smooth and saccadic eye movements discriminated between the different levels of target acceleration for the longer initial visible ramp durations, we sought to determine how the response of these two systems (i.e., total eye displacement) during the occlusion interval was

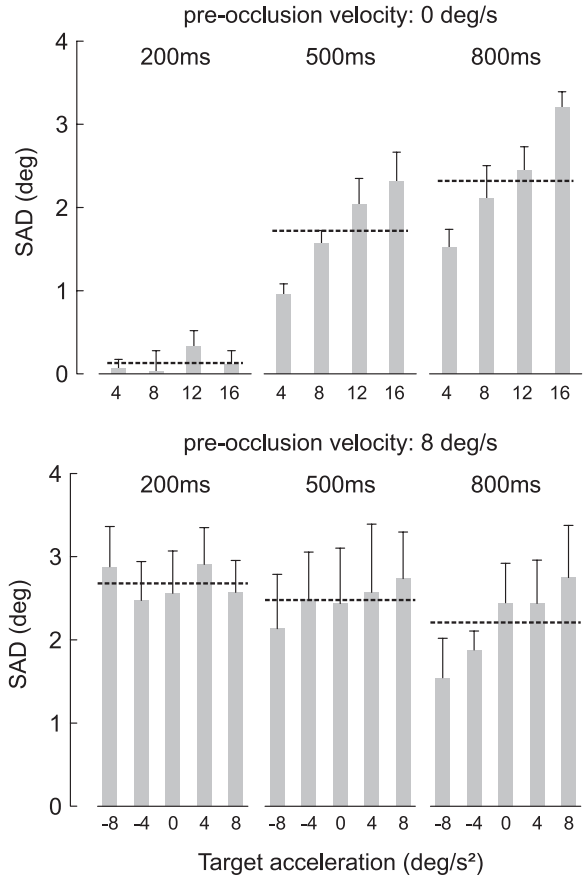

FIG. 5. Group mean (+SE) saccadic eye displacement (SAD, light gray bars) during the transient occlusion for targets with 0 deg/s preocclusion velocity (*top*) and 8 deg/s preocclusion velocity (*bottom*). Horizontal dashed lines represent the mean SAD obtained by collapsing the data across all target accelerations. *Left*, *middle*, and *right columns* (i.e., subset of bars) correspond, respectively, to initial ramp duration of 200, 500, and 800 ms. Horizontal axis legends represent target acceleration.

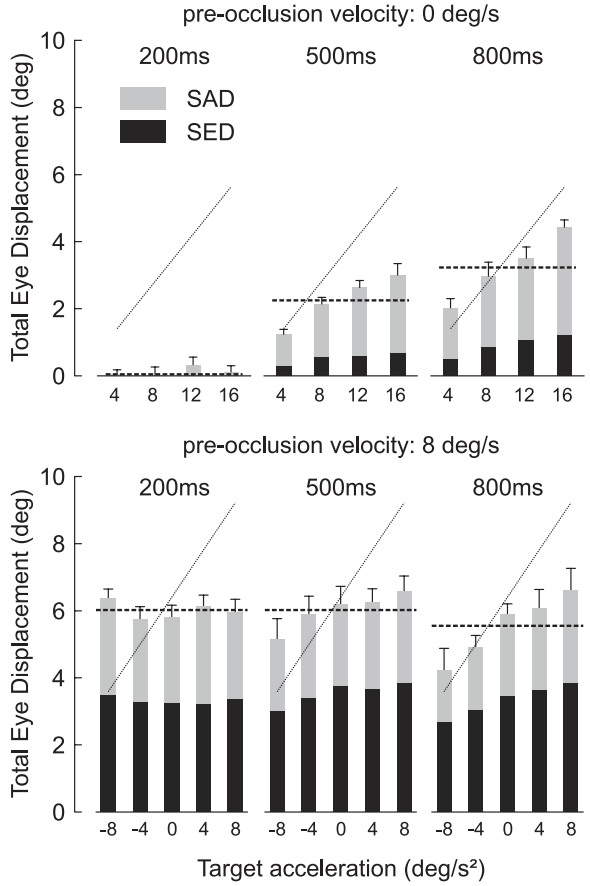

FIG. 6. Group mean (+SE) total eye displacement during the occlusion interval for target with 0 deg/s preocclusion velocity (*top*) and 8 deg/s preocclusion velocity (*bottom*). Diagonal lines represent target displacement. Dark and light gray bars represent contribution to displacement from smooth eye displacement (SED) and SAD, respectively. Horizontal dashed lines represent the mean total eye displacement obtained by collapsing the data across all target accelerations. *Left*, *middle*, and *right columns* (i.e., subset of bars) correspond, respectively, to initial ramp duration of 200, 500, and 800 ms. Horizontal axis legends represent target acceleration.

combined in an attempt to match the target displacement. Again, the average total eye displacement was computed (horizontal dashed lines in Fig. 6) and compared with the response to each acceleration level. This revealed a significant interaction between ramp duration and target acceleration for both the 0 and 8 deg/s preocclusion velocity conditions [$F(6,30) = 5.34$, $P < 0.01$, $F(8,40) = 3.47$, $P < 0.01$, respectively]. Group mean data in Fig. 6 (*left column*) show that, as expected given the findings for the measures of smooth and saccadic eye motion reported earlier, total eye displacement did not differ with target acceleration for an initial ramp duration of 200 ms. There was a complete lack of eye displacement from either smooth pursuit or saccades during the occlusion interval for the 0 deg/s preocclusion target velocity (*top*), which resulted in total eye displacement close to zero. For the 8 deg/s condition (*bottom*), there was substantial eye displacement during the occlusion for the 200-ms ramp duration; however, there was no difference in total eye displacement across the different levels of target acceleration. Conversely, the *middle* and *right columns* of Fig. 6 show that when the target was initially presented for 500 or 800 ms, total eye displacement differed according to target acceleration for both the 0 deg/s (*top*) and

8 deg/s (*bottom*) preocclusion velocity conditions. The regression statistics shown in Table 1 indicate that the change in total eye displacement was proportional to target acceleration in presentations with 500- or 800-ms initial ramp. Still, across all initial ramp durations, the combined response from SAD and SED failed to match well the target displacement for the higher levels of acceleration (e.g., 4 and 8 deg/s^2 for the 8 deg/s preocclusion target velocity) and resulted in significant undershoot.

Comparison of the individual contribution from the saccadic and smooth pursuit system to total eye displacement for the 0 deg/s preocclusion target velocity shows that when there was substantial eye motion during the occlusion interval (500- and 800-ms ramps) this was dominated by the saccadic system. Averaged over the different target accelerations, there was 3.3- (500-ms ramp) and 2.6-fold (800-ms ramp) more contribution from saccades than from smooth pursuit to total eye displacement. In contrast, comparison of the individual contribution from the saccadic and smooth pursuit systems to total eye displacement for the 8 deg/s preocclusion target velocity indicated that eye motion during the occlusion interval was not dominated by one eye movement system. Averaged over the different target accelerations, there was 0.8 (200-ms ramp), 0.7 (500-ms ramp), and 0.7 (800-ms ramp) times less contribution from saccades than from smooth pursuit to total eye displacement.

DISCUSSION

In this study we investigated the ocular pursuit response of human subjects to accelerating target motion. To determine whether the drive underlying ocular pursuit is modified according to an on-line prediction of target acceleration made during pursuit of the initial visible ramp, we examined smooth and saccadic eye movements during the transient occlusion of a moving target. A combination of target parameters was chosen that enabled us to disambiguate whether ocular pursuit was driven according to target acceleration or to a measure of target velocity. Specifically, we arranged presentations such that target velocity just before the transient occlusion did not differ with target acceleration and was thus not related to the ensuing target velocity. This design enabled us to distinguish between the following three hypotheses. First, if subjects based their extrapolation on the preocclusion target velocity, their oculomotor response should not change in accord with target acceleration (final velocity hypothesis). Second, if the oculomotor response were based on the mean target velocity of any period of the initial visible ramp, it would be negatively related with target acceleration (mean velocity hypothesis). Third, if the extrapolated response during the transient occlusion were based on the different levels of target acceleration (acceleration hypothesis), this should be reflected in the smooth and saccadic eye movements.

In line with previous studies of human ocular pursuit (Becker and Fuchs 1985; Bennett and Barnes 2003, 2005; Orban de Xivry et al. 2006), we observed that a combination of smooth pursuit eye movements and saccades was made in response to the disappearance of a moving target. Importantly, and consistent with the acceleration hypothesis, we found that both types of eye movement showed signs of acceleration discrimination when target motion was visible for $\geq$500 ms. During the initial, visible part of the target motion leading up to the transient occlusion, the smooth eye velocity was appropriately scaled to target velocity (0 or 8 deg/s) generated by the different levels of target acceleration (4, 8, 12, 16 or -8, -4, 0, 4, 8 deg/s^2). The smooth eye velocity then deflected from its preocclusion trajectory, but recovered to a level that was positively scaled, albeit with some error in absolute magnitude, to target velocity at reappearance. This would not have been expected if smooth eye velocity were controlled using a measure of target velocity taken just before the transient occlusion (final velocity hypothesis). Furthermore, the difference in recovery for each level of target acceleration was not consistent with an extrapolation based on a measure of mean target velocity during the initial ramp, which was negatively related to target acceleration (mean velocity hypothesis). [1]

In the longer presentations where there was evidence of scaling the oculomotor response to target acceleration, there was still significant retinal slip when target acceleration was -8 to 8 deg/s^2. These results are qualitatively similar to those from our previous work in which we found no difference between start-occlusion and end-occlusion eye velocity when presentations of accelerating target motion (4 and 8 deg/s^2) were received in random order (Bennett and Barnes 2006). Thus it would seem that, although information related to target acceleration can be extracted on-line during the initial visible ramp, the process is not entirely sufficient to drive the predictive oculomotor response in the absence of visual input. This contrasts with the improved tracking of an occluded accelerating target that is presented in blocked order, where there is a strong expectation in advance of the upcoming target motion (Bennett and Barnes 2006).

In addition to the effects on smooth pursuit, the saccadic eye displacement (SAD) was also positively related to target acceleration in presentations with the longer initial visible ramp durations. For presentations in which the preocclusion target velocity was 0 or 8 deg/s after 500 or 800 ms of target motion, there was a difference in SAD during the transient occlusion between the most extreme levels of target acceleration. In other words, subjects exhibited more saccadic eye displacement in presentations where the target displacement was only partially compensated by the smooth eye displacement (SED). Consistent with our previous work (Orban de Xivry et al. 2006), it would appear that the smooth and saccadic eye movements work in combination to maintain eye displacement toward the trajectory defined by target acceleration, even in the absence of the target. Further support for this notion was evident in the proportional contribution made by the saccadic and smooth pursuit systems to total eye displacement during the transient occlusion. In presentations with 0 deg/s preocclusion target velocity, subjects responded with relatively little SED during the transient occlusion. This is probably explained by the fact that they had to first reverse the smooth eye movement and then slowly build it up again during the transient occlusion. Nonetheless, subjects compensated for the lack of smooth eye displacement with a large contribution from the saccadic system. Conversely, when the preocclusion target velocity was 8 deg/s, subjects exhibited a similar contribution from smooth eye displacement and saccadic eye displacement.

[1] It is worth commenting that, although the extraocular muscle system has second-order dynamic properties (Robinson 1981), which might result in some continuation of eye motion after occlusion, the effects would not last for more than about 20–30 ms and thus cannot explain the scaling of eye velocity to target velocity at the end of the transient occlusion.

Interestingly, despite showing greater smooth eye displacement in presentations with preocclusion target velocity of 8 deg/s compared with 0 deg/s, in combination with SAD this was not sufficient to eliminate the position error at the moment of target reappearance for the 4 and 8 deg/s^2 targets (Fig. 6). This might seem surprising given that the contribution from saccades was not particularly large. However, there are several reasons why this might have occurred. First, it is possible that by using a relatively short occlusion interval, subjects did not have sufficient time to exhibit more than one or two saccades (see Bennett and Barnes 2005). Second, it is important to remember that subjects were instructed to maintain pursuit of the target during the transient occlusion and, as such, it would not have been appropriate to make particularly large saccades that took the eye toward the predicted reappearance position and thus long way off the occluded trajectory. Finally, and related to both of the preceding scenarios, it is possible that subjects had only a relatively primitive prediction regarding the upcoming target motion because the experimental design permitted this to be formed on-line only during pursuit of the initial visible ramp.

Together, the observed smooth and saccadic eye movements provide clear evidence that subjects extracted target acceleration on-line when the initial visible ramp was $\geq$500 ms and used this to control pursuit before and during the transient occlusion. It would appear that an initial exposure of 200 ms was insufficient to perform these operations. First, there was a lack of scaling of eye velocity to target velocity leading up to the transient occlusion. Second, and most important, the lack of scaling observed leading up to the transient occlusion was still evident at the moment of target reappearance. For presentations with 0 deg/s preocclusion target velocity, target displacement had changed by a further 1.62 to 6.6 deg, whereas target velocity had increased between 3.6 and 14.4 deg/s (4 and 16 deg/s^2). These values are well within the range of established displacement (Watamaniuk and Heinen 1999) and velocity (McKee 1981) sensitivity. Still, eye displacement and velocity did not change during the occlusion interval and therefore failed to match the corresponding characteristics of target motion (Fig. 6). For presentations with 8 deg/s preocclusion target velocity, eye displacement and velocity changed by a similar amount during the occlusion interval. This shows that even when there was sufficient time to exhibit a recovery during the transient occlusion, an initial ramp of 200 ms was not sufficient to discriminate target acceleration and use this to accurately control the oculomotor response.[2] Instead, subjects exhibited a default response that provided a reasonable balance between overshooting and undershooting the different target trajectories experienced in the experiment, which is consistent with the final velocity hypothesis.

Our finding that ocular pursuit does not scale to target acceleration after an initial 200-ms ramp indicates that the temporal limits of this process are longer than those required to extract target velocity. Evidence concerning the time to extract velocity comes from experiments by Lisberger (1998), who examined normal pursuit initiation, which is often characterized by the occurrence of an initial saccade with a latency of approximately 200 ms. Lisberger demonstrated that, although presaccadic smooth eye velocity was much lower than the target, postsaccadic smooth eye velocity closely matched target velocity, implying that target velocity had been effectively extracted during the first 200 ms. Interestingly, though, our finding that 200 ms was not sufficient to scale ocular pursuit to target acceleration is in accord with the temporal limits of acceleration discrimination reported in psychophysical studies. For example, it has been shown that perceptual discrimination of target acceleration for an absolute judgment task (i.e., judge acceleration per se and not whether acceleration differs between presentations) is more accurate when the target motion is presented for 600 compared with 300 ms (see Fig. 3 in Brouwer et al. 2002). Indirectly, then, results of the present study provide further evidence for the suggestion that pursuit and perception share inputs from a common motion-processing stage (Beutter and Stone 1998; Madelain and Krauzlis 2003; Stone and Krauzlis 2003).

If it is accepted that the processing of accelerating motion in humans is not achieved directly by acceleration sensitive cells, it follows that on-line extraction of acceleration could be achieved indirectly through a process of sequential sampling of the velocity signal. This requires a mechanism in which velocity information from the immediate past is temporarily stored so that it can be "compared" with current velocity. There is evidence for such behavior from motion-perception tasks (Greenlee et al. 1995). The notion of sampling and temporarily storing velocity information is also one that we have previously put forward to explain the ability to make anticipatory smooth pursuit movements (Barnes and Asselman 1991), which can be scaled to several different levels of velocity presented in a sequence (Barnes and Schmid 2002; Collins and Barnes 2005). In addition, we have shown that a good approximation to the acceleration/deceleration characteristics of sinusoidal target motion can be achieved by sampling and storing velocity information from a single half cycle at 250-ms intervals (Barnes 1994; Barnes et al. 2000). Most recently, we proposed a modified version of this process, which enabled us to generate realistic simulations of the smooth pursuit eye movements made in response to an accelerating motion signal that underwent a transient occlusion (Bennett and Barnes 2006). The results of the present study are consistent with the general logic of this approach to representing velocity-based information and indicate that, at least for the control of ocular pursuit, 200 ms is insufficient to acquire the minimum of two samples required for this process.[3] As we have previously acknowledged, using on-line prediction demands a different mode of operation to

[2] For these presentations, the percentage change in target velocity during the initial visible ramp was below the reported 25% discrimination threshold (Brouwer et al. 2002; Gottsdanker et al. 1961; Schmerler 1976). Therefore, it could be argued that information on target acceleration may have been extracted over 200 ms had the change in velocity exceeded 25%. However, it should be borne in mind that this was not the case when preocclusion target velocity was 0 deg/s. Here, the combination of target parameters resulted in a 200% change in target velocity yet subjects did not show any evidence of scaling in their pursuit response to the different levels of target acceleration.

[3] For presentations with an initial ramp duration of 200 ms and preocclusion target velocity of 0 and 8 deg/s, our stimuli had initial velocities that ranged between 0.6 and 2.4 deg/s (4, 8, 12, 16 deg/s^2) and 9.2 and 6.8 deg/s ($-$8, $-$4, 0, 4, 8 deg/s^2). In this respect, our stimuli covered a range of the preferred speeds of neurons in MT (Lisberger and Movshon 1999), the monkey homologue of the human motion processing area V5/V5a. In addition, our presentations with an initial ramp duration of 500 or 800 ms (preocclusion target velocity of 0 and 8 deg/s) had a similar range of initial velocities. Therefore, it would seem unlikely that the range of target velocities examined can account for the duration effect on the ability to scale ocular pursuit.

that where subjects have a very clear expectation of the upcoming target motion characteristics in advance of the presentation. By randomizing presentation order and using several different combinations of target motion characteristics, it would be behaviorally unrealistic for subjects to generate a persistent representation of the upcoming target motion that could be fed forward to the oculomotor controller. Instead, if subjects were to predict the upcoming target motion, this would have to be generated on-line by extracting the relevant velocity and acceleration signal from the initial visible ramp. Here, it is crucial to emphasize the point that on-line prediction does not equate to using an efference copy to perpetuate eye motion. For human ocular pursuit, efference copy–based models are unnecessarily restrictive and do not account well for voluntary influences. Moreover, in such models, efference copy reflects only the most recent eye velocity and thus does not incorporate information regarding target acceleration. As we have shown in the present study, eye velocity at 50 ms into the transient occlusion does not relate well to eye velocity at the end of the transient occlusion. We suggest that on-line prediction may be an early stage in the process of representing target motion, whereby the comparison between two or more velocity samples provides only an approximation of the future target motion.

GRANTS

This work was supported by the Leverhulme Trust (United Kingdom), the Medical Research Council, the Fonds National de la Recherche Scientifique, the Fondation pour la Recherche Scientifique Médicale, the Belgian Program on Interuniversity Attraction Poles initiated by the Belgian Federal Science Policy Office, and an internal research grant from Fonds Spéciaux de Recherche of the Université Catholique de Louvain and the European Space Agency of the European Union. The scientific responsibility rests with its authors.

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